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### Inia geoffrensis. By Robin C. Best and Vera M. F. da Silva

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### Inia D'Orbigny, 1834

Inia D'Orbigny, 1834:31. Type species, Inia boliviensis, by monotypy. Gervais (1855) transferred the species Delphinus geoffrensis (de Blainville, 1817) to the genus Inia. I. boliviensis is here treated as a subspecies of I. geoffrensis.

CONTEXT AND CONTENT. Order Cetacea, Suborder Odontoceti, Superfamily Platanistoidea, Family Iniidae. The genus *Inia* is monotypic.

## Inia geoffrensis (de Blainville, 1817) Boto

Delphinus Geoffrensis de Blainville, 1817:151. Type locality "South America, probably upper Amazon of Brazil."

Delphinus Geoffroyi Desmarest, 1822:512. Emendation of geoffrensis Blainville.

Delphinus frontatus Cuvier, 1823:278. Type locality "unknown origin, presumably South America."

Delphinus amazonicus von Spix and Martius, 1831:1118 and 1133. Type locality "Amazon River."

Inia Boliviensis D'Orbigny, 1834:31. Type locality "... du Fort du Principe de Beira ...," Iteñez River, Bolivia.

Delphinus Inia von Rapp, 1837:47. New name for Inia boliviensis d'Orbigny.

Inia geoffrensis Gervais, 1855:92. First use of present name combination.

**CONTEXT AND CONTENT.** Context as in the generic summary. There are three currently recognized subspecies.

I. g. boliviensis D'Orbigny, 1834. Type locality Rio Guaporé, (=Iteñez) near Principe da Beira (which is in Brazil). See van Bree and Robineau, 1973:662

 g. geoffrensis (de Blainville). Type locality lower Rio Negro or lower Amazon, see van Bree and Robineau, 1973:662.

I. g. humboldtiana, Pilleri and Gihr, 1977:63. Type locality from San Fernando de Apuré, Venezuela.

**DIAGNOSIS.** Inia geoffrensis is distinguished from other platanistids by the presence of short bristles on the top of the long and robust beak, by having two types of teeth (heterodonty), and by the boat-keel shape of the elongate dorsal fin (Best and da Silva, 1989a; Layne, 1958; Layne and Caldwell, 1964).

The skin color of adults (which may be uniformly pink or blotched pink), the pronounced mobility of the head and flippers, and the diving behavior distinguish *I. geoffrensis* from other Odontoceti, including *Sotalia*, the only sympatric dolphin (Best and da Silva, 1989a, 1989b; Layne, 1958; Layne and Caldwell, 1964; Martin, 1990; Pilleri, 1969). The skull has a slight degree of skewness or asymmetry (Ness, 1967), usually with a slight torsion of the rostrum and mandibles, both laterally and dorsoventrally (Best and da Silva, 1989b; Casinos and Puigdefabregas, 1981).

GENERAL CHARACTERS. 1. geoffrensis is the largest of the river dolphins (Fig. 1). Recorded maxima for length and mass are 2.55 m and 160 kg for males and 2.01 m and 98.5 kg for females in Brazil (Best and da Silva, 1984, 1989a, 1989b); 2.74 m for a male in Peru (Layne, 1958); and 2.16 m for a female in Bolivia (Pilleri and Gihr, 1977).

The body is corpulent and heavy, but extremely flexible, capable of bending and twisting. Measurements of *I. geoffrensis* from the Apure River were: length of body, 124-228 cm; length of flippers, 29-42 cm; width of flippers, 13-21 cm; length of dorsal fin, 30-61 cm; and width of flukes, 34-54 cm (Pilleri and Gihr, 1977; Trebbau, 1975).

Young animals are slate-gray. The body coloration of adults probably depends on temperature, clarity of the water, and possibly geographical location (Layne, 1958; Miranda-Ribeiro, 1943; Trebbau, 1975). Adult *I. geoffrensis* that live in opaque rivers tend to be predominantly pink. In rivers where light penetration is greater, all age classes are dark, showing, at most, a pink flush on the underside and flanks (Best and da Silva, 1989a, 1989b; Layne, 1958; Layne and Caldwell, 1964; Trebbau, 1975; Trebbau and van Bree, 1974). An albino female from San Fernando de Apure, Venezuela, was caught and kept in captivity for >1 year (von Gewalt, 1978).

The rostrum is prominent and robust, the melon relatively small and flaccid, but it can be altered in shape by muscular control (Penner and Murchison, 1970). The eyes are small and inconspicuous. The pectoral fins are large, broad, and paddle-like, and flukes are broad and triangular. There is no distinct dorsal fin, but an elongate dorsal keel extends from the mid-body to the strongly keeled caudal peduncle (Fig. 1).

**DISTRIBUTION.** I. geoffrensis is widely distributed and endemic to the Amazon and Orinoco river basins. The principal limits to its distribution seem to be impassable rapids, waterfalls, and very small or shallow rivers (Fig. 2).

Inia g. humboldtiana is found in the Orinoco basin, in all parts of the main river (Hershkovitz, 1963; Meade and Koehnken, 1991; Pilleri, 1979; Pilleri and Gihr, 1977; Pilleri and Pilleri, 1982; von Humboldt, 1889). The largest continuous area of the Orinoco basin uninhabited by I. geoffrensis is possibly the Caroni river basin (Venezuela) which is blocked near its mouth by waterfalls and, since the 1960s, by the Gury dam (Meade and Koehnken, 1991). I. g. humboldtiana is found in the waters that drain the upland Guyana Shields but not in the northernmost parts of the Guyana Shields, and throughout the Branco and Tacutu Rivers along the frontiers between Guyana and Brazil (Meade and Koehnken, 1991; Pilleri and Gihr, 1977). It is also in the Rio Negro (Brazil) above São Gabriel da Cachoeira and throughout the Cassiquiare Canal (Best and da Silva, 1989a, 1989b). Botos are as far upriver as La Esmeralda on the Orinoco River (Wallace, 1853), on the Isla de Margarita, Venezuela (Trebbau and van Bree, 1974). I. g. geoffrensis is found in the Amazon river system, occurring from the delta, near Belém (Pine, 1973), into the principal tributaries of the Solimões River, the Tocantins as far upstream as the Araguaia River and its tributaries, the Branco, and the Negro. I. g. geoffrensis are in the lower Xingú River (but not below Altamira; Carvalho, 1949), the Tapajós River, above the rapids near São Luiz do Tapajós (Lamb,



Fig. 1. Live adult male *Inia geoffrensis* from Lago Tefé, Japurá River, Amazon, Brazil. Length of body is 190.5 cm.

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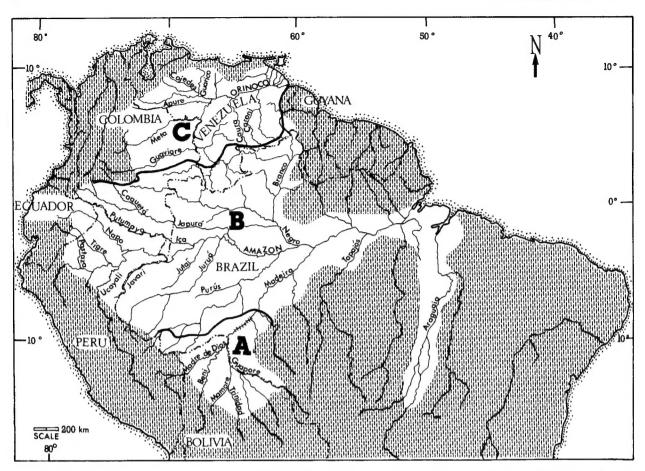


Fig. 2. Distribution of *Inia geoffrensis*. A: *Inia g. boliviensis*, upper Madeira River and Beni system in Bolivia; B: *Inia g. geoffrensis*, Central Amazon; C: *I. g. humboldtiana*, Orinoco Basin.

1954), and above the rapids of Teotonio in the Madeira River. In Peru, they are found in the Ucayali, Pucalpa, Saimira, Marañon (to the mouth of the Cenepa), and Santiago rivers. In Ecuador, the species occurs in the Napo, Tigre, Pastaza, and Santiago rivers (Guallart, 1962; Kasuya and Kajihara, 1974; Pilleri and Gihr, 1977). I. g. boliviensis occurs in the upper Madeira River and in the Ichilo, Mamoré, Ipurupuru, Iboré, Baré, and Guaporé rivers (D'Orbigny, 1834; Pilleri and Gihr, 1969, 1977). The 200 km stretch of rapids between Porto Velho and Guajará-Mirim is probably a barrier to I. g. geoffrensis (Casinos and Ocaña, 1979; Grabbert, 1983; Pilleri and Gihr, 1977, 1981).

FOSSIL RECORD. Miranda-Ribeiro (1943) described a tooth of *Plicodontina mourai* from the Juruá River (Brazil) and suggested that this animal was a close ancestor of *I. geoffrensis*. He compared the *P. mourai* tooth with a Pleistocene tooth of *Saurodelphis argentinus* from Argentina and suggested that close similarities existed between these two genera. *I. geoffrensis* may have entered the Amazon basin from the Pacific before the Andean orogeny, some 15 mya (Grabbert, 1983), but other authors postulate a more recent entry from the Atlantic (Brooks et al., 1981; Gaskin, 1982).

FORM. The skull (Fig. 3) is long-snouted and robust. The mandibles are fused for about one-third of their total length (D'Orbigny, 1834; Flower, 1869; Miranda-Ribeiro, 1943). The existence of condylus tertius has been recorded (van Bree and Trebbau, 1974).

The number of teeth per ramus varies from 22 to 35. Teeth are conical in the anterior half of each tooth-row, whereas those in the posterior half have a lingual flange that extends from each crown towards the labial side and a depression in the lingual side. All teeth have a rugose outer surface that is caused by a gentle wrinkling of the enamel and are often discolored, ranging from light-yellow to a tar-brown color. They may be chipped, anomalous in growth, and diseased (Best and da Silva, 1989a, 1989b; Ness, 1966; Pilleri and Gihr, 1969).

The vertebral formula of 48 specimens of *I. geoffrensis* from the Central Amazon is: 7C (atlas and axis non-fused), 13T, 3L, and Ca 16-19, total 39-42 (Best and da Silva, 1989b). There are 13 pairs of ribs and the sternum is a single bone. A total of 40 vertebrae and 8-9 chevron bones were found in two specimens from Bolivia (Pilleri and Gihr, 1977). The pectoral girdle is unique in that the scapula and sternum are secondarily attached, forming the shoulder joint. The humerus is long, resulting in a system of attachment that allows an extreme degree of motility of the flippers (Klima et al., 1980). A sixth phalange is often present in the manus (Flower, 1869; Leisewitz, 1921; Lönnberg, 1928; Miranda-Ribeiro, 1943; Pilleri and Gihr, 1976; van Bree and Trebbau, 1974).

The brain is smaller in structure than in other odontocetes. The brain/body mass ratio is  $0.014 \pm 0.001$  (n = 3; Gruenberger, 1970; Pilleri and Gihr, 1969).

Acoustic nerves and quadrigeminal bodies are large, implying well-developed acoustic capabilities, in contrast to the reduced size of the optic nerve fibers (Morgane and Jacobs, 1972). The sphincter about the eye is restricted, giving the impression that the eye is extremely small. The cornea is large and protruding and is highly vascularized (Pilleri, 1977). The pupil is round, and the crystalline lens and cornea yellow (Dawson, 1980; Dral, 1981). No tapetum is present and the retina is duplex, with rod-type receptors being more common than cone-type receptors (Waller, 1982). Vision is good in clear water (Phillips and McCain, 1964).

The nasal tract is typically complex, in that the blowhole slit is concave in the caudal direction. There are two lateral vestibular sacs which are almost symmetrical, although the right sac is dorsally positioned relative to the left (Mead, 1975; Schenkkan, 1977).

Inia geoffrensis, when compared with Pontoporia and Platanista, has a relatively large papilla dermic and an external layer of keratin (Arvy, 1977a). The stratum of Inia's skin may have intercellular lipids to avoid the hydration of the stratum externum (Geraci et al., 1986).

The stomach is multi-chambered, with a saccular forestomach

separated from the muscular esophagus by a 1–2-cm opening. The lining of the forestomach is similar to that of the esophagus, which has a well-defined juncture with the main stomach. The main stomach lining is typically dark red and covered with 1.5-cm folds. There is a 1-cm opening in its apical right-side that leads to the pyloric stomach, which is about 3 by 5 cm (Best and da Silva, 1989b; da Silva, 1983, 1986; Kito and Yamasaki, 1985; Yamasaki and Kamiya, 1981; Zhou et al., 1982). The length of the intestine (in m) is  $4.598 \pm 15.299 \times$  body length (da Silva, 1983).

Selected organ masses (in g) from animals of 14.5-156.0 kg body mass are: left kidney, 42-265 (n=23); left lung, 183-2,835 (n=23); adrenal, 1.7-10.0 (n=6); heart, 58-640, and liver, 359-4,140 (Best and da Silva, 1989b). The masses of organs of a male 1.87 m long from Peru were: liver, 1,800 g; heart, 275 g; both kidneys, 300 g; spleen, 23 g; lungs, 1,450 g; adrenal, 9 g; and thymus, 75 g (Layne and Caldwell, 1964).

FUNCTION. Hemoglobin varies from 13.3 to 14 g/dl and there is one electrophoretic component (Baluda et al., 1972; de Monte and Pilleri, 1969; Knoll, 1932; Lenfant, 1969; Ridgway et al., 1970; Ridgway, 1972). Sodium chloride and osmolarity values are low, and blood uric acid levels are high (6.3–16.5 mg/dl) compared to other freshwater and marine dolphins (Ridgway et al., 1970; Tobayama and Kamiya, 1989). Oxygen binding capacity is low compared with other cetacea, with 18.8 ml % hematocrit and 14.3 gm % hemoglobin (Lenfant, 1969).

The respiratory interval is from 1.5 to 0.5 min (Layne, 1958; Layne and Caldwell, 1964; Penner and Murchison, 1970; Ridgway, 1972; Trebbau, 1975) and may be as short as 0.3 min in a newborn calf (Caldwell and Caldwell, 1972). Tobayama and Kamiya (1989) recorded respiratory intervals from 5 to 134 s, with a mean of 42.8 s for a male and 31.3 s for a female. There is no apparent rhythm to the respiratory cycle and a series of long dives may be followed by one, or several, short dives (Best and da Silva, 1989b).

Heart rate of an adult male in transport was 60 beats/min and of a small male, shortly before death, 96 beats/min. Rectal temperature of the latter animal was 36.3°C (Layne and Caldwell, 1964). Heart rate of another adult male was 57-78 beats/min and its rectal temperature was 35.4°-36.6°C (Tobayama and Kamiya, 1989).

Inia geoffrensis does not possess isovaleric acids (Litchfield et al., 1975). The biochemical topography of melon lipids indicates an inner (with a posterior node associated with the right nasal plug) and an outer melon. This, together with melon anatomy and the voluntary muscular control of melon shape, are the main factors in the directioning of echolocation beams (Litchfield and Greenberg, 1979), although the shape of the pterygoids is also involved in directionality (Pilleri et al., 1979).

ONTOGENY AND REPRODUCTION. In the central Amazon region, male I. geoffrensis reach sexual maturity at a body length of about 198 cm. The combined testicular mass of mature males exceeds 0.4% of body mass. Testis size increases curvilinearly with length of body (Best and da Silva, 1984, 1989b). Based on the presence of corpora lutea in the ovaries, females are thought to reach sexual maturity from 160 to 175 cm in body length and ovulation occurs with equal frequency in both ovaries, which are relatively large and rounded (Best and da Silva, 1984, 1989b). The corpus luteum is not pedunculated (Harrison and Brownell, 1971). Individuals that are concurrently pregnant and lactating have been recorded (Best and da Silva, 1984, 1989b; Harrison and Brownell, 1971). Pregnancy is externally discernable 4 months prior to birth by distention anterior to the genital slit. Birth takes 1.5-5 h and presentation is typically caudal. Estrus is indicated by distended labia (Huffman, 1970).

Births coincide with peak levels of water in rivers and their initial recession from May to July. The body length of the calf at birth is estimated as  $79.4\pm3.5$  cm (range 66-81). Gestation is estimated to be 8.5 months (Best and da Silva, 1984). Young animals in captivity grow up to 20.7 cm/year (Caldwell et al., 1966). The fetus and newborn calf have a series of vibrissae on parts of the rostrum that persist throughout life (Arvy, 1977b).

One female captured with a young calf was still lactating 1 year later. The composition of her milk was: dry matter, 20.3%; protein, 7.6%; lactose, 3.4%; ash, 0.7%; and fat, 13.0% (von Gewalt, 1978).



Fig. 3. Dorsal, ventral, and lateral view of the skull, and lateral and dorsal view of the mandible of adult male *Inia geoffrensis*. Condilobasal length is 557 mm.

ECOLOGY. I. geoffrensis appears to be less abundant in the Orinoco River than in the Amazon River (Best and da Silva, 1989a, 1989b; Kasuya and Kajihara, 1974). In a boat survey from Manaus to Tefé (ca. 550 km), overall density was  $0.19 \pm 0.66$ /km (Magnusson et al., 1980). An average density of  $0.22 \pm 0.04$  animals/km was found in four surveys from Manaus to Tabatinga (ca. 1,525 km) when the mean number of dolphins observed was  $340 \pm 67.3$ / survey (Best and da Silva, 1989a, 1989b). Estimates of density for the rivers Ichilo (1 dolphin/4 km), Ipurupuru (1/0.9 km) and Ibaré (1/1.0 km) in Bolivia were given by Pilleri (1969) and Pilleri and Gihr (1977). Observation on the rivers near Iquitos (Peru) yielded boto densities of 1.8/h and 27/h from the Orinoco and Meta rivers (no effort data available; Kasuya and Kajihara, 1974).

Inia geoffrensis is found in all riverine habitat types in the Orinoco and Amazon basins, except estuaries and large rapids or waterfalls (da Silva, 1983; Layne, 1958). The species seems to occur in nearly all types of microhabitats, such as main rivers, small channels, lakes, at the mouths of rivers, and just below rapids. During the dry season, animals may be restricted to large deepwater lakes and main river channels. When the rivers rise, they can be found in flooded areas, grassland, and forests, even swimming among flooded trees (da Silva, 1986; Layne, 1958).

Seasonal migrations are related to the migration of fish and the annual flooding cycle of the river (da Silva, 1986). Botos have undefended home ranges, and seasonal movements are probably slight shifts in the boundaries of the core area (Best and da Silva, 1989a, 1989b). I. geoffrensis from the central Amazon region

(Negro and Tocantins rivers) occupy the same range year-round (Best and da Silva, 1989b; Trebbau, 1975). Near Leticia (Peru), these animals have a diurnal pattern to their movements (Layne, 1958).

No records of any natural predation of *Inia geoffrensis* exist although black caimans (*Melanosuchus niger*), bull sharks (*Carcarhinus leucas*) and jaguars (*Panthera onca*) are potentially capable of taking botos (Best, 1984; Best and da Silva, 1989b). Small, crescent-shaped wounds on the skin of *I. geoffrensis* sometimes attributed to piranhas (Serrasalmidae) and catfish of the family Loricariidae (Trebbau, 1975; von Gewalt, 1978), are actually caused by small catfish of the families Cetopsidae and Trichomycteridae (Best and da Silva, 1989b).

Inia geoffrensis has a diet unique among the Cetacea in that its heterodont dentition allows it to tackle and crush armoured prey. A total of 43 species of 19 families of fish were found in the stomachs of botos in the central Amazon, of which 57% were freshwater croaker (Plagioscion spp.). The mean body length of fish eaten is 20 cm (range 5-80 cm). The greatest diversity of diet occurs during high water levels. Some selectivity is shown during the dry season when the water level is low and the fish are more concentrated (Best, 1984; Best and da Silva, 1989a, 1989b; da Silva, 1983, 1986).

Inia geoffrensis eat piranhas (Serrasalmidae; de Carvalho, 1961), pacus (Myleus sp.; Layne and Caldwell, 1964), characins (Pilleri, 1977), catfish (Phractocephalus hemiliopterus; Trebbau and van Bree, 1974), river turtle (Podocnemis sextuberculata; da Silva and Best, 1982), and crab, Poppiana argentiniana (Pilleri, 1972). Food consumption rates of nine captive animals range from 2.2 to 4.0% of body mass/day with a mean of  $3.1 \pm 0.5\%$  (da Silva, 1983).

Most parasitic worms described for *I. geoffrensis* are host-specific. The only exception is the trematode *Pholeter gastrophilus*, which is known also from marine dolphins (Dailey and Brownell, 1972; Gibson and Harris, 1979; Zam et al., 1970). The trematodes *Hunterotrema caballeroi*, *H. macrossoma*, or *Halocerus* sp. (McIntosh, 1960) may be responsible for some of the respiratory problems which are common both in wild and captive *I. geoffrensis* (Layne and Caldwell, 1964; Woodard et al., 1969). The nematode *Preitrachelius* (=*Anisakis*) insignis has been recorded from *I. geoffrensis* (Sprent, 1982), but not from the sympatric *Sotalia* (Best and da Silva, 1989b).

Large quantities of the nematode P. insignis invariably occur in the stomach, but there is no evidence that the infections were pathological (Best and da Silva, 1989b). One pathogenic infection, the golf-ball disease caused by Streptococcus iniae, has been recorded (Pier and Madin, 1976) as has the fungal infection Candida albicans (von Gewalt, 1978; Layne and Caldwell, 1964; Ostenrath, 1976). Other health problems include acute pancreatitis, adrenal failure, chronic nephritis, and cutaneous gout (Garman et al., 1983; Testi and Pilleri, 1970; Trebbau, 1975). Broken bones, deformed and broken mandibles and rostrum (Pilleri and Gihr, 1969), dental anomalies such as alveolar fusion and dystopia lingual (Casinos and Puigdefabregas, 1981; Pilleri and Gihr, 1969), and dental conditions considered to be caries (Ness, 1966) are reported. Among other observed pathologies are synechia anterior (Dral et al., 1980), pseudoarthrosis of the humerus, and hyperostosis of the radio-ulna (Pilleri and Gihr, 1969).

Causes of mortality in captive animals include ulcerated stomach, occluded lumen of one-third of the intestine, degenerated spleen, ulcerated bladder wall, and congestive heart failure (Trebbau, 1975).

The lampara seine, as well as fixed and floating gill-nets, pose threats to the populations in the Amazon River (Best and da Silva, 1989a, 1989b). The development of hydroelectric power in the Amazon and Orinoco rivers drastically reduces abundance of fish fauna (Ferreira, 1984) and breaks the continuity of the population, dangerously isolating small genepools in individual reservoirs (e.g., the Guri Dam in Venezuela; Pilleri, 1979).

Mercury, used in the refining of fluvial gold, has been found in high concentration in fish identified as part of *Inia*'s diet (Best and da Silva, 1989a, 1989b; Pfeiffer and Lacerda, 1988). Milk from one *I. geoffrensis* contained 1.22 ppm DDT, 1.52 ppm PCBs and 0.036 ppm Dieldrin (von Gewalt, 1978).

Longevity in captivity ranges from 10 to 26 years (von Gewalt, pers. comm.; Tobayama and Kamiya, 1989; P. St. John, pers. comm.). *Inia geoffrensis* have given birth twice in captivity. In both cases the calves died, one a few minutes after birth and the other after 2 weeks (Caldwell and Caldwell, 1972; Huffman, 1970). An important aspect of husbandry is the maintenance of a stable social

group; failure to do so may result in the death of subordinate animals (Sylvestre, 1985).

Wild *I. geoffrensis* associate with other mammals including the tucuxi (*Sotalia fluviatilis*; da Silva, 1983), the giant otter (*Pteronura brasiliensis*; Defler, 1983), and man (Lamb, 1954; Trebbau, 1975), particularly with respect to fishing, catching or driving fish inshore. Another complex relationship is that of fisherman using the dolphins to locate fish schools (Goulding, 1979).

BEHAVIOR. I. geoffrensis is usually solitary; 58-81% of individuals were observed alone (Best and da Silva, 1989a, 1989b; Kasuya and Kajihara, 1974; Layne, 1958; Magnusson et al., 1980). I. geoffrensis are rarely seen in cohesive groups of more than three individuals, even though loose aggregations may be seen in feeding areas or involved in courtship and mating. Most groups of two individuals (involving about 12-26% of all animals seen) are mother and calf pairs (Best and da Silva, 1989b; Layne, 1958).

Inia geoffrensis react protectively to injured or captured individuals (von Gewalt, 1978; Layne, 1958; Pilleri, 1969; Trebbau, 1975). Succorant (mother-calf) behavior has been recorded in the wild (Trebbau, 1975) and in captivity where a female and young remained inseparable for 3 years (Caldwell and Caldwell, 1972).

In captivity, this species has not established a social hierarchy through aggression (Caldwell and Caldwell, 1969a, 1969b; Caldwell et al., 1989; Layne and Caldwell, 1964; Spotte, 1967). However, most aquaria reported problems of intraspecific aggression (Caldwell et al., 1989) sometimes leading to death (Sylvestre, 1985).

Masturbation is common in captive males. Females try to insert objects into the genital slit or press it against an object (Layne and Caldwell, 1964; Pilleri et al., 1980; von Gewalt, 1979).

Sexual foreplay is apparently initiated by the male nibbling the female's flipper and flukes. If not receptive, the female becomes aggressive toward the male, but he may try to copulate regardless. Copulation may be frequent (e.g., 47 times in 3 h 23 min). Three main copulatory positions have been recorded: right angle ventral to ventral (58%), parallel head to head (32%), and head to tail (10%), with the animals oriented in opposite directions. Insertions average 25 s and range from 4 to 115 s. Contractions may occur at least 24 h prior to a birth that takes from 4 to 5 h while the female swims in rapid, tight circles. Intervals between contractions vary from 1 to 29 min, averaging 7.5 min. At birth the umbilical cord breaks next to the body of the calf and normally the female immediately helps the calf to the surface. The calf nurses at about 30 min intervals. The placenta is expelled some 5 h after birth and is eaten by the mother (Caldwell and Caldwell, 1972; Huffman, 1970).

Basic sounds produced by *I. geoffrensis* are click trains, single intense clicks, and burst pulses (Caldwell et al., 1966; Norris et al., 1972). The clicks are 16-170 kHz with peak energy around 60-80 kHz (Evans, 1973; Kamminga and Weirsma, 1981; Weirsma, 1982). *I. geoffrensis* shows the same wave shape and frequency spectrum as *Tursiops* (Kamminga, 1979), where a dominant frequency is around 45 kHz with a half power bandwidth of about 15 kHz, although few echolocation clicks were found at <40 kHz and none were <25 kHz (Evans, 1973; Penner and Murchison, 1970). Ten distinct calls were described from captive individuals (Caldwell et al., 1966): echolocation-like run, grate, creaking door sounds, squawk, screech, bark, whimper, squeak, squeaky-squawk, crack, and jaw-snap. The presence of whistles is unclear (Caldwell et al., 1966; Caldwell and Caldwell, 1970; Nakasai and Takemura, 1975).

The narrow sonar beam extends in the median plane from  $+30^{\circ}$  to  $-20^{\circ}$  around the axis of the rostrum (Pilleri et al., 1979). Another type of acoustic signal is a loud respiratory exhalation that is made when the dolphin is alarmed or uneasy (Layne and Caldwell, 1964). Auditory sensitivity is from 1 to 105 kHz with the greatest response from 75 to 90 kHz (Jacobs and Hall, 1971).

Inia geoffrensis are slow swimmers with usual speeds of 2.4-5.1 km/h, but bursts of >22.5 km/h (Cabrera and Yepes, 1940; Klima et al., 1980; Layne, 1958; Layne and Caldwell, 1964; Pilleri, 1969). As they are often found above rapids, the species must be capable of strong swimming for some length of time (Best and da Silva, 1989b).

Surfacing characteristics of *I. geoffrensis* vary from a shallow type, in which the melon, the tip of the rostrum, and the long dorsal ridge are out of the water simultaneously, to a high-arching roll in which these parts appear sequentially with the dorsum thrust well

out of the water. The tail is rarely raised out of the water prior to a dive (Layne and Caldwell, 1964; Pilleri, 1969).

Captive *I. geoffrensis* rarely show any fear of strange objects, have a strong curiosity, and are playful (Caldwell et al., 1966; Huffman, 1970). *I. geoffrensis* had the lowest trainability among 11 species studied in its capacity to be controlled by auditory signals rather than by touch signals (Defran and Pryor, 1980). *I. geoffrensis* were also less timid than other cetaceans of similar size and comparatively low on the scale of social contact, aggressive behavior, play, and aerial display. Food was a more powerful reinforcer than human contact (Braden et al., 1973).

In the wild, although I. geoffrensis feeds both diurnally and nocturnally, fishing activity peaks at 0600-0900 h and 1500-1600 h (Best and da Silva, 1989 $\dot{b}$ ). Fish are taken by the anterior teeth, transferred to the stronger posterior teeth, crushed, and swallowed head first (Layne and Caldwell, 1964; da Silva, 1983). Larger fish are torn to pieces and the head is shaken off before ingestion (da Silva, 1983). Fishing is usually done close to shore, in shallow bays, in flooded forests, or where two rivers meet. Human fishing operations and the disruption of fish schools caused by water turbulence are used as means of making fishing easier (Best, 1984; Best and da Silva, 1989a, 1989b; da Silva, 1983). I. geoffrensis may swim close to boats travelling near the riverbank to catch disturbed fish (da Silva, 1983; Lamb, 1954; Trebbau, 1975). Although often a solitary feeder, loose groups can fish in a coordinated fashion by herding and attacking schools (da Silva, 1983; Defler, 1983; Goulding, 1979). Food sharing has been recorded among captive I. geoffrensis (Johnson, 1982) and may occur in the wild as well (da Silva, 1983).

Botos may sleep in a stationary, often upside down, position, with eyes closed (Caldwell et al., 1966; Caldwell and Caldwell, 1969b; Layne and Caldwell, 1964; Penner and Murchison, 1970; Pilleri, 1969; Sylvestre, 1985). A wild *I. geoffrensis* was observed lying motionless on the bottom with its eyes closed (Best and da Silva, 1989b).

In captivity I. geoffrensis play with inanimate objects and living animals, throw objects above the surface, and interact with other dolphins by passing objects and inventing games (Caldwell et al., 1989; Layne and Caldwell, 1964; Pilleri et al., 1980; Sylvestre, 1985; von Gewalt, 1979). Wild animals pull grass underwater, throw sticks, and play with logs (Best and da Silva, 1989b; Layne, 1958; Layne and Caldwell, 1964). In interspecific play, captive I. geoffrensis swam synchronously around the tank and played nip and chase. In the wild, interaction with the sympatric dolphin S. fluviatilis is rare, but a calf I. geoffrensis was seen to roll repeatedly across the back of an adult Sotalia (Best and da Silva, 1989b). Intraspecific play involves chasing, ambushing, swimming in echelon, passing objects, and placing the rostrum between the jaws of another animal. Wild Inia also flipper wave, show the head or tail above the surface, lob-tail and, rarely, jump clear of the water (Best and da Silva, 1989b; Caldwell et al., 1989).

Inia geoffrensis readily associate with man and are playful, sometimes retrieving thrown objects and even soliciting physical contact. When swimming, dolphins may nip divers, play tag or take the diver's hand under its flipper and tow him or embrace him (Layne and Caldwell, 1964). Wild botos grasp fishermen's paddles, rub against canoes, and may become quite tame (Best and da Silva, 1989b; da Silva, 1990; Lamb, 1954).

**GENETICS.** The diploid chromosome number is 44, sex determination is by XY chromosomes, and this species is cytogenetically similar to other odontocetes, with the exception of the sperm whale (*P. macrocephalus*; Kulu et al., 1971). Balanced translocation in *I. geoffrensis* without apparent phenotypic abnormality has been observed (Duffield, 1977).

REMARKS. A single species is currently recognized. On the basis of color, length-mass ratio, cranial characters, number of teeth, shape of sternum, brain size, and haemoglobin motility, Pilleri and Gihr (1977, 1981) proposed the adoption of two species *Inia boliviensis* and *Inia geoffrensis* for 2 geographically separate groups. This distinction was contested on the grounds that the characters used are too variable to be taxonomically useful and that the sample sizes were small (Casinos and Ocaña, 1979).

Inia geoffrensis has many vernacular names, the most common being boto, bufeo, and tonina. The name Inia derives from the Guarayos tribe in Bolivia (D'Orbigny, 1834). The Portuguese name boto has been consistently misspelled in the English language through

the use of the phonetic spelling boutu (Mitchell, 1975; Nowak and Paradiso, 1983; Rice, 1977). The proper spelling boto (Miranda-Ribeiro, 1943), should be adopted in future publications (Best and da Silva. 1989a; 1989b).

Inia geoffrensis is listed on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and became protected in Brazil in 1986.

Inia geoffrensis is generally protected from human interference by legends that associate them with supernatural powers (Bates, 1962; Miranda-Ribeiro, 1943; da Silva, 1990). It is believed that the spirit of drowned persons enters the bodies of botos and that these animals change into handsome young men (Pine, 1973). Consequently there has been no directed hunting of this dolphin anywhere in its range, with the possible exception of the Portuguese colonists using oil for illumination (Ferreira, 1794). When captured accidentally in fishing nets, if alive, I. geoffrensis are usually released, although they may be harpooned if disturbing fishing operations. When found dead in nets, eyes and genitalia are removed to be sold as love charms. The fat is sometimes used as an asthma cure or lamp oil and teeth as amulets to ward off aches, particularly toothaches. Amazonian people do not use the meat or skin of botos (da Câmara-Cascudo, 1954; de Carvalho, 1963; da Silva, 1990).

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Robin C. Best passed away on December 17, 1986.

#### LITERATURE CITED

ARVY, L. 1977a. La peau, le phanere et leurs parasites chez les cetacés. Vie et Milieu, Series A, 27:137-190.

——. 1977b. Les precurseurs en cetologie et les cetacés. Vie et Milieu, Series A, 6:277-288.

BALUDA, M. C., D. D. KULU, AND R. S. PARKES. 1972. Cetacean haemoglobins: electrophoretic findings in nine species. Comparative Biochemistry and Physiology, 41B:647-653.

BATES, H. W. 1962. The naturalist on the River Amazon. University of California Press, Los Angeles, 465 pp.

BEST, R. C. 1984. The aquatic mammals and reptiles of the Amazon. Pp. 371-412, in The Amazon. Limnology and landscape ecology of a mighty tropical river and its basins (H. Sioli, ed.). Dr. W. Junk Publisher, Dordrecht, 763 pp.

BEST, R. C., AND V. M. F. DA SILVA. 1984. Preliminary analysis of reproductive parameters of the boutu, *Inia geoffrensis*, and the tucuxi, *Sotalia fluviatilis*, in the Amazon River system. Pp. 361-369. Reports of the International Whaling Commis-

sion, Special Issue 6, 495 pp.

1989a. Biology, status and conservation of Inia geoffrensis in the Amazon and Orinoco river basin. Pp. 23-34, in Biology and conservation of the river dolphins (W. F. Perrin, R. L. Brownell, Jr., Zhou Kaiya, and Liu Jiankang, eds.). International Union for Conservation of Nature and Natural Resources (IUCN), Species Survival Commission, Occasional Paper 3, 173 pp.

. 1989b. Amazon river dolphin, Boto. Inia geoffrensis (de Blainville, 1817). Pp. 1-23, in Handbook of marine mammals (S. H. Ridgway and R. J. Harrison, eds.). Academic Press,

London, 442 pp.

Braden, I. C., C. Conklin, and E. W. Friedman. 1973. Food and human contact as reinforcers in the Amazon river dolphin (*Inia geoffrensis*). Pp. 871-872 in Proceedings of the 81st Annual Congress of the American Psychology Association.

BROOKS, D. R., T. B. THORSON, AND M. A. MAYER. 1981. Freshwater stingrays (Potamotrygonidae) and their helminth parasites: testing hypotheses of evolution and coevolution. Pp. 147-175, in Advances in cladistics (V. A. Funk and D. R. Brooks, eds.). New York Botanic Garden. New York.

eds.). New York Botanic Garden, New York.

CABRERA, A., AND J. YEPES. 1940. Mamíferos Sud-Americanos
(Vida, costumbres y description). Historia Natural Ediar, Buenos Aires, 370 pp.

CALDWELL, M. C., AND D. K. CALDWELL. 1969a. The ugly dolphin. Sea Frontiers, 15:308-314.

——. 1969b. More about . . . the ugly dolphin. Sea Frontiers, 15:349-355.

- -. 1970. Further studies on audible vocalisations of the Amazon freshwater dolphin, Inia geoffrensis. Los Angeles County Museum Contribution in Science, 187:1-5.
- 1972. The littlest ugly dolphin. Sea Frontiers, 18:24-29
- CALDWELL, M. C., D. K. CALDWELL, AND W. E. EVANS. 1966. Sounds and behaviour of captive Amazon freshwater dolphins Inia geoffrensis. Los Angeles County Museum Contribution in Science, 108:1-24.
- CALDWELL, M. C., D. K. CALDWELL, AND R. L. BRILL. 1989. Inia geoffrensis in captivity in the United States. Pp. 35-41, in Biology and conservation of the river dolphins (W. F. Perrin, R. L. Brownell, Jr., Zhou Kaiya, and Liu Jiankang, eds.). International Union for Conservation of Nature and Natural Resources (IUCN), Species Survival Commission, Occasional
- Paper 3, 173 pp. Carvalho, J. C. M. 1949. Observações Zoológicas Antropológicas na Região dos formadores do Xingú. Revista do Museu Nactional do Rio de Janeiro, 1:7-9.
- CASINOS, A., AND J. OCAÑA. 1979. A craniometrical study of the genus Inia d'Orbigny, 1834 (Cetacea, Platanistoidea). Saugetierkundliche Mitteilungen, 27:194-206.
- CASINOS, A., AND J. N. PUIGDEFABREGAS. 1981. Novos dados sobre anomalies cranianes a Inia geoffrensis (Cetacea, Platanistidae). Butlleti de la Societat Catalana de Biologia, 5-6:223-228.
- CUVIER, G. 1812. Rapport sur divers cetacés. Annales du Musée d'Histoire Naturel de Paris, 19:10.
- 1823. Recherches sur les ossements fossiles, où l'on retablit les caracteres de plusieurs animaux dont les resolutions du globe ont detruit les espéces. G. Dufour et E. D'Ocagne Libraires, Paris, 405 pp.
- D'Orbigny, M. A. 1834. Notice sur un nouveau genre de cetacé des rivieres du centre de l'Amerique meridionale. Noveau Annales du Musee d'Histoire Naturel de Paris, 3:28-36.
- DA CÂMARA-CASCUDO, L. 1954. Dicionário do folclore brasileiro. Ministério Educação e Cultura, Instituto Nacional do Livro, Rio de Janeiro, 415 pp.
- Dailey, M. D., and R. L. Brownell, Jr. 1972. A checklist of marine mammal parasites. Pp. 528-576, in Mammals of the sea. Biology and medicine (S. A. Ridgway, ed.). Charles C Thomas Publisher, Springfield, Illinois, 812 pp.
- DA SILVA, V. M. F. 1983. Ecologia alimentar dos golfinhos da Amazonia. M.Sc. thesis, University of Amazonas, Manaus, Brasil, 118 pp.
- . 1986. Comportamento de alimentação dos golfinhos de água doce, Inia geoffrensis e Sotalia fluviatilis com considerações sobre a pesca comercial. Pp. 215-227, in Actas de la Primera Reunion de Trabajo de Expertos en Mamíferos Acuáticos de America del Sur, Buenos Aires, 236 pp.
- -. 1990. Botos, mitológicos hóspedes da Amazônia. Ciência
- Hoje, 11:14-18.

  DA SILVA, V. M. F., AND R. C. BEST. 1982. Amazon river dolphin (Inia) preys on turtle (Podocnemis). Investigations on Cetacea,
- DAWSON, W. W. 1980. The cetacean eye. Pp. 53-100, in Cetacean behaviour: mechanisms and functions (L. M. Herman, ed.). John Wiley and Sons Publisher, New York, 463 pp
- DE BLAINVILLE, H. M. D. DE. 1817. Nouveau Dictionnaire d'His-
- toire Naturelle (A. G. Desmaret, ed.). Paris, 9:152. DE CARVALHO, C. T. 1961. Esboço mastofaunístico do Território do Rio Branco. Revista de Biologia Tropical, 9:1-15.
- 1963. O boto para os habitantes do Amazonas é uma criatura sobrenatural. Fauna, 22:40-41.
- DE MONTE, T., AND G. PILLERI. 1969. Relative mobility of the haemoglobin of some cetaceans, determined by electrophoresis on cellulose acetate gel. Investigations on Cetacea, 1:173-177
- DEFLER, T. R. 1983. Associations of the giant river otter (Pteronura brasiliensis) with fresh-water dolphin (Inia geoffrensis). Journal of Mammalogy, 64:692.
- DEFRAN, R. H., AND K. PRYOR. 1980. The behaviour and training of cetaceans in captivity. Pp. 319-362, in Cetacean behaviour: mechanisms and functions (L. M. Herman, ed.). John Wiley and Sons Publisher, New York, 463 pp.
- Desmarest, A. G. 1822. Mamiferes. Pp. 512-516, in A. de Miranda-Ribeiro. 1943. Arquivos do Museu Nacional do Rio de Janeiro, 27:58 pp.

- DRAL, A. D. G. 1981. Opthalmoscopical observations on the Amazon dolphin, Inia geoffrensis. Aquatic Mammals, 8:40.
- DRAL, A. D. G., F. C. STADES, AND A. W. VAN FOREEST. 1980. Some cases of synechia anterior in aquatic mammals. Aquatic Mammals, 8:11-15.
- DUFFIELD, D. A. 1977. Phylokaryotypic evaluation of the Cetacea. Ph.D. dissert., University of California, Los Angeles, 154 pp.
- EVANS, W. E. 1973. Echolocation by marine delphinids and one species of fresh-water dolphin. Journal of the Acoustical Society of America, 54:191-199.
- 1794. Viagens Filosóficas pelas capitanias do FERREIRA, A. R. Grão Pará, Rio Negro, Mato Grosso e Cuiabá. Reedited by Conselho Federal de Cultura, São Paulo, in 1974, 246 pp.
- FERREIRA, E. J. G. 1984. A ictiofauna da Represa Hidrelétrica de Curuá-Una, Santarém, Pará. I-Lista e distribuição das espécies. Amazoniana, 8:351-363.
- FLOWER, W. H. 1869. Description of the skeleton of Inia geoffrensis and of the skull of Pontoporia blainvillei, with remarks on the systematic position of these animals in the order Cetacea. Transactions of the Zoological Society of London, 6:87-116.
- GARMAN, R. H., M. F. J. NUZZI, AND J. R. GERACI. 1983. Cutaneous gout in an Amazon dolphin. Journal of the American Veterinary Medical Association, 183:1292-1294.
- GASKIN, D. E. 1982. The ecology of whales and dolphins. Heinemann Educational Books Ltd., 459 pp.
- GERACI, J. R., D. J. St. Aubin, and B. D. Hicks. 1986. The epidermis of odontocetes: a view from within, Pp. 3-21, in Research on dolphins (M. M. Bryden and R. Harrison, eds.). University Press, New York, 478 pp.
- GERVAIS, M. P. 1855. Description des trois species de dauphins qui vivent dans la region du haut Amazone. Pp. 90-92, in F. De Castelnau, Expedition dans les parties centrales de L'Amerique du Sud, du Rio de Janeiro a Lima et de Lima au Pará,
- 7, Zoology (P. Bertrand, ed.). Paris, 480 pp.
  GIBSON, D. I., AND E. A. HARRIS. 1979. The helminth parasites of cetaceans in the collection of the British Museum (Natural History). Investigations on Cetacea, 10:309-324.
- GOULDING, M. 1979. Ecologia da pesca do rio Madeira. Falangola Editora, Belém, 172 pp.
- GRABBERT, H. 1983. Migration and speciation of the South American Iniidae (Cetacea, Mammalia). Sonderdruck aus Zeitschrift fuer Saeugetierkunde, 49:334-341.
- 1970. On the cerebral anatomy of the GRUENBERGER, H. B. Amazon dolphin Inia geoffrensis. Investigations on Cetacea, 2:129-143.
- GUALLART, S. J. 1962. Nomenclatura Jibara-Aguaruna de espécies de mamíferos en el alto Marañon. Biota, 4:155-164.
- HARRISON, R. J., AND R. L. BROWNELL, JR. 1971. The gonads of the South American dolphins Inia geoffrensis, Pontoporia blainvillei and Sotalia fluviatilis. Journal of Mammalogy, 52: 413-419.
- HERSHKOVITZ, P. 1963. Notes on South American dolphins of the genera Inia, Sotalia and Tursiops. Journal of Mammalogy, 44:98-103.
- HUFFMAN, W. E. 1970. Notes on the first captive conception and live birth of an Amazon dolphin in North America. Underwater Naturalist, 6:9-11.
- JACOBS, D. W., AND J. D. HALL. 1971. Auditory thresholds of a freshwater dolphin, Inia geoffrensis Blainville. Journal of the Acoustical Society of America, 51:530-533.
- JOHNSON, R. H. 1982. Food-sharing behavior in captive Amazon river dolphin (Inia geoffrensis). Cetology, 43:1-2.
- KAMMINGA, C. 1979. Remarks on dominant frequencies of cetacean sonar. Aquatic Mammals, 7:93-100.
- KAMMINGA, C., AND H. WEIRSMA. 1981. Investigations on cetacean sonar II. Acoustical similarities and differences in odontocete sonar signals. Aquatic Mammals, 8:41-62.
- KASUYA, T., AND T. KAJIHARA. 1974. Ecology of dolphins in the Amazon and Orinoco system. Pp. 7-11, in Scientific expedition of La Plata and Amazonian dolphins. University of Tokyo, Freshwater Dolphin Expedition, Tokyo, 93 pp. (in Japanese).
- KITO, K., AND T. YAMASAKI. 1985. Duodenal portion of the hepato-pancreatic duct of the bouto, Inia geoffrensis. Scientific Report of the Whales Research Institute (Tokyo), 36:89-95.
- KLIMA, M. H., O. OELSCHLAGER, AND D. WUNSCH. 1980. Morphology of the pectoral girdle in the Amazon dolphin Inia geoffrensis with special reference to the shoulder joint and the

7

- movements of the flippers. Sonderdruck aus Zeitschrift fuer Saeugetierkunde, 45:288-309.
- KNOLL, W. 1932. Untersuchungen ueber die Morphologie des Saeugetierblutes. Folia Haematologica, 47:201–219.
- KULU, D. D., I. VEOMATT, AND R. S. SPARKES. 1971. Cytogenetic comparison of four species of cetaceans. Journal of Mammalogy, 52:828-832.
- LAMB, B. F. 1954. The fisherman's porpoise. Natural History, 63:231-232.
- LAYNE, J. N. 1958. Observations on freshwater dolphins in the upper Amazon. Journal of Mammalogy, 39:1-22.
- LAYNE, J. N., AND D. K. CALDWELL. 1964. Behaviour of the Amazon dolphin *Inia geoffrensis* (Blainville), in captivity. Zoologica, 49:81-107.
- LENFANT, C. 1969. Physiological properties of blood of marine mammals. Pp. 95-116, in The biology of marine mammals (H. T. Andersen, ed.). Academic Press, New York, 511 pp.
- LEISEWITZ, W. 1921. Ueber en Handskelett mit sechs fingem bei dem Amazonas-Delphin (*Inia amazonica* Martius). Sitzungsberichte der Gesamten Morphologische Physiologie München, 33:1-6.
- LITCHFIELD, C., AND A. J. GREENBERG. 1979. Compositional topography of melon lipids in the Amazon River dolphin *Inia* geoffrensis: implications for echolocation. Comparative Biochemistry and Physiology, 63A:183-187.
- LITCHFIELD, C., A. J. GREENBERG, D. K. CALDWELL, M. C. CALDWELL, J. C. SIFOS, AND R. G. ACKMAN. 1975. Comparative lipid patterns in acoustical and nonacoustical fatty tissue of dolphins, porpoises and toothed whales. Comparative Biochemistry and Physiology, 63B:591-597.
- LÖNNBERG, E. 1928. Some remarks on a skeleton of *Inia geof-frensis* Blainville. Arkiv Zoologi, 20A:1-3.
- MAGNUSSON, W. E., R. C. BEST, AND V. M. F. DA SILVA. 1980. Number and behaviour of Amazon dolphin, *Inia geoffrensis* and *Sotalia fluviatilis* in the Rio Solimões, Brasil. Aquatic Mammals, 8:27-32.
- MARTIN, A. R. 1990. Whales and dolphins. Salamander Books, London, 192 pp.
- McIntosh, A. 1960. A new campulid trematode, Hunterotrema caballeroi, n. gen. n. sp., from an Amazon dolphin, Inia geoffrensis, Pp. 207-208, in Libro Homenaje al Dr. Edwardo Caballero Y Caballero Jubileo 1930-1960.
- Mead, J. G. 1975. Anatomy of the external nasal passages and facial complex in the Delphinidae (Mammalia: Cetacea). Smithsonian Contribution to Zoology, 207:1–72.

  Meade, R. H., and L. Koehnken. 1991. Distribution of the river
- MEADE, R. H., AND L. KOEHNKEN. 1991. Distribution of the river dolphin, tonina *Inia geoffrensis*, in the Orinoco river basin of Venezuela and Colombia. Interciencia, 16:300-312.
- Venezuela and Colombia. Interciencia, 16:300-312.

  MIRANDA-RIBEIRO, A. 1943. Inia geoffrensis (Blainville) Boto vermelho; boto branco; golfinho do Amazonas; piraiaguara. Arquivos do Museu Nacional do Rio de Janeiro, 37:23-58.
- MITCHELL, E. 1975. Porpoise, dolphin and small whale fisheries of the world. Status and problems. International Union for Conservation of Nature and Natural Resources (IUCN) Monograph, 2:1-125.
- MORGANE, P. J., AND M. S. JACOBS. 1972. Comparative anatomy of the cetacean nervous system. Pp. 118-244, in Functional anatomy of marine mammals, Vol. 1 (R. J. Harrison, ed.). Academic Press, London, 451 pp.
- NAKASAI, K., AND A. TAKEMURA. 1975. Studies on the underwater sounds—VI. On the underwater calls of freshwater dolphins in South America. Bulletin Faculty Fisheries of Nagasaki University, 40:7-13.
- NESS, A. R. 1966. Dental caries in the Platanistidae whale Inia geoffrensis. Journal of Comparative Pathology, 76:271-279.
- . 1967. A measure of symmetry of the skulls of odontocete whales. Journal of Zoology (London), 153:209-221.
- NORRIS, K. S., G. W. HARVEY, L. A. BUZNELL, AND T. D. K. KARTHA. 1972. Sound production in the freshwater porpoises Sotalia fluviatilis Gervais and Deville, and Inia geoffrensis Blainville, in the Rio Negro, Brasil. Investigations on Cetacea, 4:251– 260.
- NOWAK, R. M., AND J. L. PARADISO. 1983. Walker's mammals of the world. Fourth ed. The Johns Hopkins University Press, Baltimore, 1:1-568, 2:569-1362.
- OSTENRATH, F. 1976. Some remarks on the therapy of mycotic

- and bacteriological skin disease in freshwater dolphins (Inia geoffrensis). Aquatic Mammals, 4:49-55.
- Penner, R. H., and A. E. Murchison. 1970. Experimentally demonstrated echolocation in the Amazon River porpoise, *Inia geoffrensis* (Blainville). Proceedings of the Seventh American Conference on Biological Sonar and Diving Mammals, 1–22, Standard Research Institute, CA, USA.
- PFEIFFER, W. C., AND L. D. DE LACERDA. 1988. Mercury inputs into the Amazon region, Brazil. Environmental Technology Letters, 9:325-330.
- PHILLIPS, J. D., AND G. McCAIN. 1964. Black-white visual discrimination in the Amazon porpoise: *Inia geoffrensis*. American Psychologist, 19:503.
- PIER, G. B., AND S. H. MADIN. 1976. Streptococcus iniae sp. nov., a beta-haemolytic streptococcus isolated from an Amazon freshwater dolphin, Inia geoffrensis. International Journal of Systematic Bacteriology, 26:93-99.
- PILLERI, G. 1969. On the behaviour of the Amazon dolphin Inia geoffrensis in Beni (Bolivia). Revue Suisse de Zoologie, 76: 58-91.
- ——. 1972. Poppiana argentinianus Rathbun, 1909 (Crustacea, Decapoda) in the stomach contents of Inia geoffrensis from Rio Ibaré, Bolivia. Investigations on Cetacea, 4:104.
- . 1977. The eye of *Pontoporia blainvillei* and *Inia boliviensis* and some remarks on the problem of regressive evolution of the eye in Platanistoidea. Investigations on Cetacea, 8:149-159.
- from the Rio Apure, Venezuela. Investigations on Cetacea, 10: 136-142.
- PILLERI, G., AND M. GIHR. 1969. Zur anatomie and Pathologie von *Inia geoffrensis* de Blainville 1817 (Cetacea, Sussuidae) aus dem Beni, Bolivien. Investigations on Cetacea, 1:96-106.
- ——. 1976. The manus of the Amazon dolphin, Inia geoffrensis (de Blainville, 1817) and remarks concerning so-called "polydactyly." Investigations on Cetacea, 7:129-137.
- d'Orbigny, 1834) and the Amazonian bufeo (Inia geoffrensis de Blainville, 1817) with a description of a new subspecies (Inia geoffrensis humboldtiana). Investigations on Cetacea, 8: 11-76.
- ——. 1981. Additional considerations on the taxonomy of the genus *Inia*. Investigations on Cetacea, 12:15-27.
- PILLERI, G., AND O. PILLERI. 1982. Zoologische Expedition Zum Orinoco und Brazo Cassiquiare 1981. Universitat Bern Hirnanatomisch Institut, Bern, 154 pp.
- PILLERI, G., K. ZBINDEN, AND C. KRAUS. 1979. The sonar field of *Inia geoffrensis*. Investigations on Cetacea, 10:147-155.
- PILLERI, G., M. GIHR, AND C. KRAUS. 1980. Play behaviour in the Indus and Orinoco dolphin (*Platanista indi* and *Inia geof* frensis). Investigations on Cetacea, 11:57-108.
- PINE, R. H. 1973. Mammals (exclusive of bats) of Belém Pará, Brazil. Acta Amazonica, 3:47-49.
- RICE, D. W. 1977. A list of the marine mammals of the world. Third ed. National Oceanic and Atmospheric Administration (NOAA), Technical Report National Marine Fisheries Service (NMFS), 711:1-13.
- RIDGWAY, S. H. 1972. Homeostasis in the aquatic environment. Pp. 590-748, in Mammals of the sea. Biology and medicine (S. H. Ridgway, ed.). Charles C Thomas, Springfield, Illinois, 812 pp.
- RIDGWAY, S. H., J. G. SIMPSON, G. S. PATTON, AND W. G. GILMARTIN. 1970. Haematologic findings in certain small cetaceans. Journal of the American Veterinary Medical Association, 157:566–575.
- SCHENKKAN, E. J. 1977. Notes on the nasal tract complex of the boutu, *Inia geoffrensis* (de Blainville, 1817) (Cetacea, Platanistidae). Beitragen tot Dierkunde, 46:275-283.
- SPOTTE, S. H. 1967. Intergeneric behaviour between captive Amazon river dolphin *Inia* and *Sotalia*. Underwater Naturalist, 4:9-13.
- SPRENT, J. F. A. 1982. Ascaridoid nematodes of South American mammals, with a definition of a new genus. Journal of Helminthology, 56:275-295.
- SYLVESTRE, J. P. 1985. Some observations on behaviour of two Orinoco dolphins (*Inia geoffrensis humboldtiana* Pilleri and

8 MAMMALIAN SPECIES 426

- Gihr, 1977) in captivity, at Duisburg Zoo. Aquatic Mammals, 11:58-65.
- TESTI, F., AND G. PILLERI. 1970. Glomerulonefrite cronica parcellare in un delphino amazonico (*Inia geoffrensis*). Attidella Societa Italiana delle Scienze Veterinarie, 24:491-493.
- Tobayama, T., and T. Kamiya. 1989. Observations on *Inia geoffrensis* and *Platanista gangetica* in captivity at Kamogawa Sea World, Japan. Pp. 42–45, in Biology and conservation of the river dolphins (W. F. Perrin, R. L. Brownell, Jr., Zhou Kaiya, and Liu Jiankang, eds.). International Union for Conservation of Nature and Natural Resources (IUCN), Species Survival Commission, Occasional Paper 3, 173 pp.
- TREBBAU, P. 1975. Measurements and some observations of the freshwater dolphin, *Inia geoffrensis*, in the Apure River, Venezuela. Zoologische Garten, Jena, 45:153-167.
- Trebbau, P., and J. H. van Bree. 1974. Notes concerning the freshwater dolphin *Inia geoffrensis* (de Blainville, 1817) in Venezuela. Zeitschrift des Saugetierk, 39:50-57.
- VAN BREE, P. J. H., AND D. ROBINEAU. 1973. Notes sur les holotype de *Inia geoffrensis* (de Blainville, 1817) et de *Inia geoffrensis* (d'Orbigny, 1834) (Cetacea, Platanistidae). Mammalia, 37: 558-664.
- VAN BREE, P. J. H., AND P. TREBBAU. 1974. Sobre algumas anomalias del esqueleto de la tonina de agua dulce *Inia geof-frensis* (de Blainville, 1817) (Cetacea, Platanistidae). Boletin Academia de Ciencias Fisicas, Matematicas, y Naturales de Venezuela, 33:3-9.
- VON GEWALT, W. 1978. Usere tonina (*Inia geoffrensis* Blainville, 1817), Expedition 1975. Zoologische Garten, Jena, 48:323-384.
- ——. 1979. Selbsterfundene Unterwasser—"Jongleur" Spiele bei *Inia geoffrensis* (de Blainville, 1817). Sonderdruck aus Zeitschrift fuer Saeugetierkunde, 44:57–58.
- VON HUMBOLDT, A. 1889. Personal narrative of travels to the equinoctial regions of America during the years 1799-1804. Translated from the French and edited by Thomasina Press, London, 3 Vol.
- VON RAPP, W. 1837. Die Cetaceen zoologisch anatomisch dan gestellt. Stuttgart und tubingen, 182 pp.

- VON SPIX, J. B., AND C. F. VON MARTIUS. 1831. Reise in Brasilien auf Befehl Sr. Majestic maximilient Joseph I, Konigs von Baiern, in der Jahren 1817 bis 1820 (Gemacht. Fleischer, eds.). Munchen, 3:1388 pp.
- WALLACE, A. R. 1853. Narrative of travels on the Amazon and Rio Negro. Reprinted in 1986 from the 1853 edition. Time-Life Books, B. V. Belgium, 541 pp.
- Waller, G. N. H. 1982. Retinal ultrastructure of the Amazon River dolphin (*Inia geoffrensis*). Aquatic Mammals, 9:17-28.
- Weirsma, H. 1982. Investigations of cetacean sonar. IV. A comparison of wave shapes of odontocete sonar signals. Aquatic Mammals, 9:57-66.
- WOODARD, J. C., S. G. ZAM, D. K. CALDWELL, AND M. C. CALDWELL. 1969. Some parasitic diseases of dolphins. Journal of Pathology Veterinary, 6:257-272.
- YAMASAKI, F. S., AND T. KAMIYA. 1981. The stomach of the boutu, *Inia geoffrensis*: comparison with those of other platanistids. Scientific Report of the Whales Research Institute (Tokyo), 33:69-81.
- ZAM, S. G., D. K. CALDWELL, AND M. C. CALDWELL. 1970. Some internal parasites from freshwater cetaceans from the upper Amazon River. Investigations on Cetacea, 2:250-251.
- ZHOU, K., LI YUEMIN, AND G. PILLERI. 1982. The digestive tract of *Inia boliviensis* (D'Orbigny, 1834). Investigations on Cetacea, 13:125-137.
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